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Feasibility of a combined sampling approach for studying caterpillar assemblages – a case study from shrubs in the Andean montane forest zone

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Abstract. We analyzed the suitability of a combined sampling approach – consisting of visual search and branch-beating – for quantifying tropical caterpillar communities. Surveys were conducted in the Ecuadorian montane forest zone, with two shrub species from the genus *Piper* serving as focal targets. We sampled 160 shrubs in the course of four experiments following a standardized sampling protocol. Subsequently each shrub was completely defoliated accompanied by an intensive leaf-by-leaf search, in an effort to extract as close to 100% of all present caterpillars as possible. We analyzed the resulting dataset with regard to completeness, taxonomical bias, and influences of daytime, complexity of shrub structure, or experience of the researcher. The standardized sampling protocol extracted between 50.6% and 71.6% of the caterpillars present on a shrub. A minor taxonomic bias of the sampling protocol was observed, but appears to be of a simple and predictable nature, and is therefore easy to account for. We did not find any significant influences of daytime. Structure and size of shrubs had a strong influence on sampling results with small and simply structured shrubs being sampled most completely, large and complex shrubs most incompletely in our dataset. Researcher experience did not appear to have an influence on the sampling efficiency or taxonomic composition of samples obtained when we compared caterpillars obtained by standardized sampling with those collected by exhaustive leaf-by-leaf search. Comparison of caterpillar sizes revealed however, that inexperienced field assistants tended to overlook large fractions of the smallest caterpillars entirely. We conclude that our standardized combined sampling approach is fairly suitable for studies concerning caterpillar communities, especially when resampling of the same shrub individuals is desired.

Keywords: Lepidoptera, *Piper*, beating tray, visual search, sampling efficiency.

Introduction

Herbivorous insects are a major fraction of all life on earth (e.g. Price, 2002). Their diversity and ecological roles have become a focus of many studies in the last decades. Lepidoptera are one of the largest taxa among this group, with currently approximately 155,000 species described (Pogue, 2009). While sampling of adults has been performed in largely identical ways for several decades, standardized sampling of their larvae is less common. Especially in the tropics, where Lepidoptera are both especially diverse and particularly poorly studied, investigation of caterpillar communities and their ecology are still in a very early stage. Projects dealing with caterpillars employ a variety of collection methods such as canopy fogging (e.g. Floren & Linsenmair, 2001), complete destructive sampling (e.g. Rodríguez-Castañeda *et al.*, 2010), visual searching (e.g. Novotny *et al.*, 2002), or branch beating (e.g. Mody & Linsenmair, 2004). Canopy fogging (Adis *et al.*, 1998) has been widely used to study canopy arthropods, however caterpillars appear to be surprisingly rare in such samples (e.g. Basset, 1991; Floren & Linsenmair, 2001) and are probably highly underrepresented. Also, with many fogging protocols, only dead specimens are retrieved, making evaluation of their ecological roles impossible. Complete destructive sampling can be expected to yield highly complete samples and allows for feeding trials, but obviously renders resampling of the same plant individual impossible.

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Visual search and branch beating are both classic, low-tech, none-invasive sampling techniques for caterpillars. Visual search allows for the recovery of well attached or concealed feeding individuals, and additionally offers the possibility to record behavioral information. Branch beating can on the other hand be expected to be more effective in the recovery of small individuals. Both methods retrieve living caterpillars and therefore allow for successive feeding trials and rearing. However, both methods are only suitable for shrubs, treelets and lower tree branches due to their limitations based on the reach of the field researcher.

We here present a combination of visual search and branch beating as standardized sampling protocol with temporal replications for immature Lepidoptera on shrubs and address various questions concerning the suitability and applicability of this sampling approach for studying caterpillar communities.

In particular we aim at testing the following specific hypotheses:

(1) Samples obtained by our combined standardized protocol retrieve the majority of individuals, but are nevertheless incomplete.

(2) Sampling efficiency is higher on shrubs with simpler structure (i.e.: fewer, larger, hairless leaves).

(3) Samples obtained by our protocol are unbiased with regard to higher taxa, feeding guilds, or size of caterpillars.

(4) Sampling efficiency of the combined standardized protocol is independent of shrub size.

(5) Sampling efficiency and composition of samples does not differ between collections taken during day and nighttime.

(6) Samples collected by operators with and without sampling experience are comparable in terms of efficiency and composition.

Methods

Study site

The study was conducted in southern Ecuador (province Zamora-Chinchipe), in the Reserva Biológica San Francisco (RBSF). This is a privately owned nature reserve adjacent to Podocarpus National Park which since 2007 forms part of the UNESCO biosphere reserve "Podocarpus-El Condor." The study area is located on the eastern slope of the Andes, where intensive ecological research has been conducted since 1997 (Beck *et al.*, 2008a). Caterpillars for the present study were sampled between 1800 and 2000m above sea level, in proximity to the Estación Científica San Francisco (3°58' S, 79°05' W). We collected data in May 2008, December 2008, February to July 2009, and October 2009.

The RBSF area is covered by nearly pristine montane rain forest (Beck *et al.*, 2008b; Homeier *et al.*, 2008). Its moth fauna has been studied intensively since 1999 by light-trapping, offering insight into patterns of moth diversity and community structure at the level of adult stages (e.g. Brehm & Fiedler, 2003; Brehm *et al.*, 2003; Fiedler *et al.*, 2008; Hilt & Fiedler, 2008). In addition, life-histories and larval host plant affiliations of geometrid moths have been studied (Brehm, 2003; Bodner *et al.*, 2010).

Study organisms

We chose two species of *Piper* for experiments. Neither of them could be formally identified yet, and they are therefore referred to with their tentative names "*Piper* sp. I" and "*Piper* sp. III" (Fig. 1). Both species have been shown to harbor a substantial caterpillar community (F. Bodner, unpublished observations), dominated by species belonging to the geometrid genus *Eois*. While both *Piper* species exhibit a shrub-like growth form with maximum sizes usually around 2-3 m (sp. I) and 2-5 m (sp. III), they differ notably in structure and complexity. *Piper* sp. I has many small twigs with many rather small leaves (average leaf size ± SD: 38.4 ± 5.5 cm^2). The undersides of the leaves are covered with thin, short hairs, especially along the leaf venation. *Piper* sp. III has a more simple structure with fewer small twigs. The leaves are larger, tougher, smooth and hairless (average leaf size ± SD: 128.4 ± 33.7 cm^2). Our sampling considered all ectophagous and semi-endophagous caterpillars of any lepidopteran family. Only stem borers and leaf miners were not searched for. Eggs and pupae of Lepidoptera were also recorded, but not included in statistical analyses.

Sampling design

The standardized sampling protocol employed in this study usually consisted of two stages. First shrubs were visually searched for lepidopteran immatures. Afterwards shrubs were beaten over a beating tray, made of 1 m^2 of white cloth mounted on the frame of an umbrella drop net, to shake further caterpillars off the shrub. This two-staged procedure was chosen to extract a maximum of lepidopteran immatures present on the shrub. Beating usually only retrieves caterpillars, especially those species which more readily drop off the shrub when disturbed or attacked. Visual searching also yields at least a part of the eggs and pupae present as well as those caterpillars which

Figure 1. The two focal shrub species (a: *Piper* sp. I; b: *Piper* sp. III) and some of the caterpillar species (c: *Eois* sp. nr. *odatis*, d: species from the *Eois olivacea* complex, e: unidentified noctuid) from this study.

cling tightly to the branches or live as concealed feeders in leaf rolls, webs or alike. During both stages sampling effort was standardized by estimated shrub volume.

Four different experiments were carried out in the course of this study (Table 1) to analyze effects of researcher experience, sampling approach, plant species, and time of day when sampling was conducted.

Standardization

We used estimated shrub volume for standardization of sampling effort. From practical reasons sampling effort was not increased linearly with shrub volume, but in steps measured as sampling effort factor (SEF). When tailoring the SEF to shrub size classes, we allowed for a larger range of shrub volumes in the higher categories, whereas for smaller shrubs a more fine grained class division was accepted. This aimed at avoiding excessive sampling effort at the upper end of the range of shrub sizes covered, or unacceptably low effort at the lower end of the size spectrum. This procedure was also implemented to balance against expected higher sampling efficiency for larger shrubs. We expected higher efficiency on larger shrubs because more leaf area can be visually searched simultaneously and more shrub volume can be accessed by individual beats. The SEF increased in the following fashion: 2 for a shrub volume of $^1/_6$ m^3, 3 for $^1/_4$ m^3 of shrub volume, 4 for $^1/_2$ m^3 of shrub volume and +1 for every further $^1/_2$ m^3 of shrub volume. For intermediate volumes SEF was adjusted to the nearest 0.5 for calculation of visual search effort only (see below).

Field work

We selected well accessible shrubs in the forest, mainly along paths, in various sizes from about 0.05

Table 1. List of experiments conducted to assess the feasibility of our sampling approach as a means of characterizing caterpillar assemblages of shrubs in the montane forest zone of southern Ecuador. Following the standardized sampling protocol, the number of remaining caterpillars present was evaluated by total defoliation of each shrub individual (Table 2).

Experiment	carried out by	standardized sampling	shrub species	sampling time	number of shrubs
P1	experienced researcher	beating	*Piper* sp. I	day only	37
P2	experienced researcher	searching and beating	*Piper* sp. I	day only	29
P3/I	inexperienced field assistants	searching and beating	*Piper* sp. I	day and night	50
P3/III	inexperienced field assistants	searching and beating	*Piper* sp. III	day and night	44

Table 2. Caterpillars obtained as $cat_{(ss)}$ and $cat_{(es)}$ in the different experiments. Mean number of caterpillars per shrub ± standard deviation are given for both $cat_{(ss)}$ and $cat_{(es)}$ for every experiment.

Experiment	$cat_{(ss)}$	Mean ± SD	$cat_{(es)}$	Mean ± SD	Efficiency
P1	91	2.46 ± 2.28	95	2.57 ± 6.47	48.9%
P2	123	4.24 ± 3.67	120	4.14 ± 4.54	50.6%
P3/I	118	2.36 ± 1.72	92	1.84 ± 1.71	56.2%
P3/III	68	1.55 ± 1.25	27	0.61 ± 0.95	71.6%
Total	400	2.50 ± 2.39	334	2.09 ± 3.96	54.5%

m^3 to about 2 m^3 volume to assess possible size effects on the efficiency of the employed sampling methods. The field sampling consisted of the following stages:
1. Estimation of shrub volume by rough measurement.
2. Spreading of white sheets of cloth around and below the plant. If necessary surrounding undergrowth was cut down to allow for smoothing of sheets.
3. Visual search of the entire target plant for lepidopteran immatures for 1 × SEF minutes (first stage of standardized sampling).
4. Beating on shrub 1 × SEF times over beating tray which was held underneath the plant (second stage of standardized sampling).
5. Checking of sheets on the ground for caterpillars that had dropped off during search or beating, but had not been caught on the beating tray.
6. Complete leaf-by-leaf defoliation of the entire shrub during which every leaf was checked individually on both sides for lepidopteran immatures.

The first two experiments (P1 and P2) were performed by the first author who has years of experience in collecting and rearing lepidopteran caterpillars (Bodner *et al.*, 2010). The other two experiments were carried out by undergraduate students without previous experience with the sampling procedure of the experiments. We chose this setup to allow for analysis of effects of previous recorder experience or training on the completeness and comparability of samples obtained.

Lab work and analysis

All caterpillars were photographed in the lab on scaled paper to allow for length measurement. All leaves of every sampled shrub were dried in an oven at 45°C for 72 hours and then weighed as a measure of available foliar biomass. For analysis, we coded caterpillars found during the two stages of the standardized protocol (stages 3 and 4) as $cat_{(ss)}$, those found outside of the standardized sampling protocol (stages 5 and 6) as $cat_{(es)}$ for exhaustive sampling. We calculated sampling efficiency as $\frac{cat_{(ss)}}{cat_{(ss)} + cat_{(es)}}$ for every experiment. Caterpillars were sorted by higher taxonomic levels (genus *Eois*, other Geometridae, other Macrolepidoptera, 'microlepidoptera') and feeding guild affiliation. True herbivores which feed on living *Piper* foliage were contrasted to non-herbivores (viz. feeding on epiphylls, lichens, mosses, or dead plant material). Data were analyzed by evaluation of contingency tables and ANOVAs calculated in Statistica 7.1 (StatSoft, 2005).

Results

In total we collected 734 caterpillars from 160 shrubs (total volume: 87.9 m^3, total dry leaf mass: 5.19 kg) in the course of the four experiments reported in this study. Of these, 400 were obtained by means of the standardized sampling approach ($cat_{(ss)}$), the remaining 334 were collected from sheets on the ground or during complete leaf-by-leaf defoliation of the shrubs ($cat_{(es)}$). The collected samples consisted mainly of members of the geometrid genus *Eois* (75.4% on *Piper* sp. I, 36.8% on *Piper* sp. III), other geometrid species (8.5% on *Piper* sp. I, 28.4% on *Piper* sp. III) and Noctuoidea (10.5% on *Piper* sp. I, 16.8% on *Piper* sp. III). While most caterpillars, especially the dominant genus *Eois*, were true herbivores (75.5%), a large fraction, notably consisting of other Geometridae and Noctuoidea, belonged to species feeding on dead leaves, lichens and other epiphylls (22.9%), as shown by extensive rearing trials (F. Bodner, unpublished observations). The remaining 1.6% of caterpillars could not be reliably assigned to either guild and were excluded from all analyses based on feeding guild affiliation. We additionally found 174 eggs and 16 pupae of Lepidoptera, but did not include them in statistical analysis as they were not the focus of the study and their samples can be expected to be far too incomplete even from exhaustive search to allow for any meaningful analysis.

The overall sampling efficiency was 54.5% for all four experiments and 56.4% for those three applying our combined sampling protocol. It ranged from 48.9% to 56.2% on *Piper* sp. I and was therefore similar for the three experiments dealing with this particular shrub species. The two experiments on this shrub species applying our combined sampling protocol (P2 and P3/I) retrieved the majority of caterpillars (50.6% and 56.2%), but only by a very narrow margin (Table 2). Sampling of shrub species *Piper* sp. III (experiment P3/III) was more effective with a yield of 71.6%. This was significantly higher ($Chi^2(DF=1) = 6.51$, $p<0.011$) than in experiment P3/I, which was performed on *Piper* sp. I under otherwise identical conditions. Comparison of $cat_{(ss)}$ and $cat_{(es)}$ on higher taxonomical levels revealed a significant bias in two of the experiments (P1 and P2), but not so in the remaining two (Table 3). The same applies to analyses based on feeding guilds. Detailed inspection of the data shows that in both cases most of the effect was due to the genus *Eois* being underrepresented in $cat_{(ss)}$. When comparing $cat_{(ss)}$ and $cat_{(es)}$ with regard to caterpillar lengths, an overall bias of the standardized sampling protocol towards larger caterpillars becomes evident (Table 4). Separate analyses of all experiments confirmed this effect only for P2 (Table 4, Fig. 2).

To analyze possible effects of shrub size on sampling efficiency, we combined all available data from the experiments on *Piper* sp. I (P1, P2 and P3/I) and assigned all shrubs to size categories by their dry leaf mass. We choose class borders in a fashion to distribute total dry leaf mass of shrubs over all categories as evenly as possible. Intermediate shrubs which did not clearly fall into one category were assigned to the one with lower total number of caterpillars. To rule out chance effects of category delimitations on the results, we performed this calculation three times, accepting 6, 7 and 8 categories, respectively. In all three cases correlation analyses of the overall sampling efficiency within each category versus the mean dry leaf mass of

Table 3. Comparison of $cat_{(ss)}$ and $cat_{(es)}$ on basis of higher taxa (genus *Eois*, other Geometridae, other Macrolepidoptera, 'microlepidoptera') and feeding guilds (herbivores, non-herbivores) by means of Pearson's Chi^2.

	Taxa		Guilds	
Experiment	Chi^2 (DF=3)	p	Chi^2 (DF=1)	p
P1	24.20	<0.00003	21.27	<0.00001
P2	8.88	<0.031	8.01	<0.005
P3/I	2.14	>0.54	1.71	>0.19
P3/III	6.01	>0.11	1.04	>0.30

Table 4. Results of ANOVAs comparing caterpillar lengths of $cat_{(ss)}$ and $cat_{(es)}$ for all experiments (Fig.2). DF: degrees of freedom.

Experiment	DF Model	DF Residual	F	p
all	1	729	15.66	<0.0001
P1	1	183	0.43	>0.51
P2	1	240	20.11	<0.0001
P3/I	1	207	2.16	>0.14
P3/III	1	93	0.97	>0.32

Table 5. Correlations of sampling efficiency with mean foliar dry weight of shrubs per category for combined data from experiments with *Piper* sp. I (P1, P2 and P3/I), split into 6 (Q6; Fig. 3), 7 (Q7) and 8 (Q8) categories, respectively.

	r	r^2	t	p
Q6	-0.9421	0.8875	5.617	0.0049
Q7	-0.8565	0.7336	3.710	0.0138
Q8	-0.7373	0.5436	2.673	0.0369

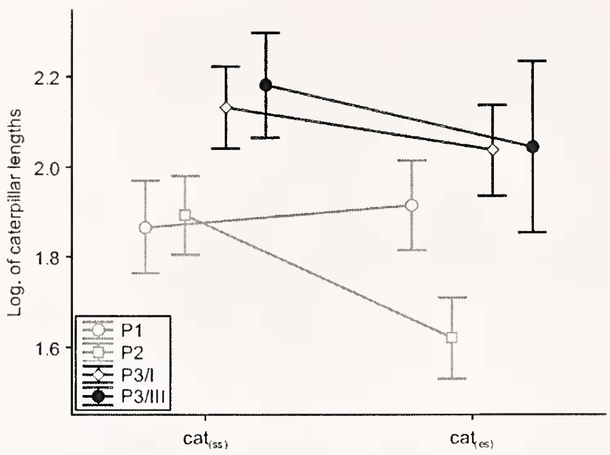

Figure 2. Average caterpillar lengths (log transformed) retrieved during the four experiments, segregated into those sampled by the standardized protocol ($cat_{(ss)}$) or during complete defoliation ($cat_{(es)}$). Whiskers are 95% confidence intervals. Grey: experiments by experienced researcher, black: experiments by field assistants. Empty symbols: *Piper* sp. I; filled symbols: *Piper* sp. III. Significance of experiment × sampling group interaction (two-way ANOVA): F(4, 723) = 5.5249, p = 0.00022.

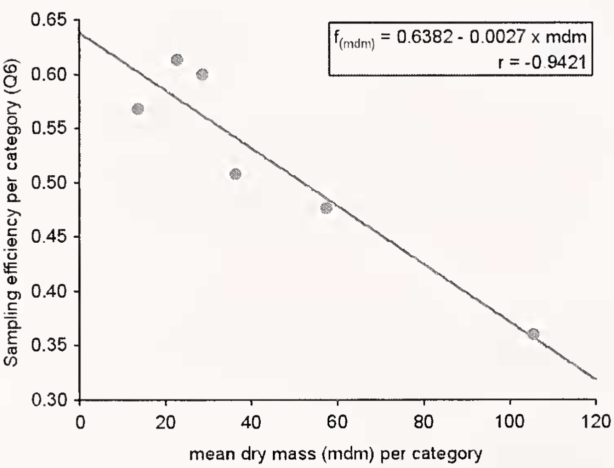

Figure 3. Relationship between sampling efficiency quotient and mean dry mass of shrubs for combined data of experiments P1, P2 and P3/I (*Piper* sp. I) split into six shrub size classes (statistical evaluation see Table 5). Regression line fitted by ordinary least squares regression.

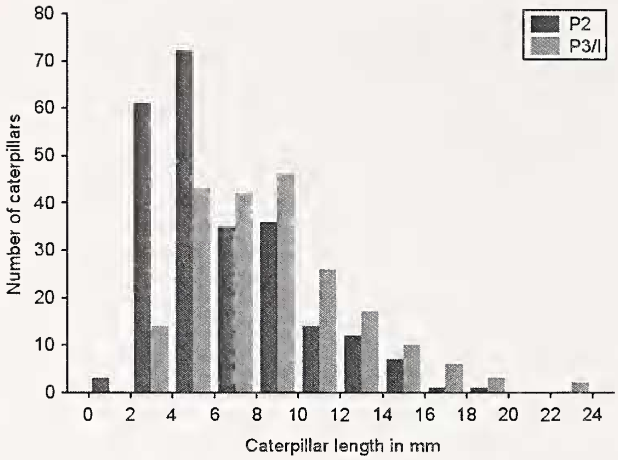

Figure 4. Frequency distributions of caterpillar lengths for experiments P2 (performed by an experienced observer, red bars) and P3/I (performed by inexperienced field assistants, blue bars) on *Piper* sp. I. Mean sizes of retrieved caterpillars differed significantly (see text). Note the difference between the experiments in the three lowest size classes.

all its shrubs showed a significantly negative effect of shrub size on sampling efficiency (Table 5, Fig. 3).

We set up contingency tables to address the question whether samples collected during day and night differ in efficiency and composition. No significant effects of collection time were observed for either sampling efficiency or sample composition on levels of higher taxa or feeding guilds ($Chi^2(DF=1)<6.68$, $p>0.06$).

Comparison of experiments P2 and P3/I with regard to the effect of recorder experience on sampling results did not reveal significant differences in sampling efficiency, or taxon or guild composition. This was true both for $cat_{(ss)}$ and for the whole dataset ($cat_{(ss)} + cat_{(es)}$) ($p \geq 0.27$). However, average size of caterpillars obtained in total was significantly smaller (F(1, 436) = 54.244, p<0.0001) when gathered by an experienced researcher (mean ± S.D. = 6.55 ± 3.30 mm) as compared to data collected by inexperienced field assistants (8.87 ± 3.91 mm; Fig. 4).

Discussion

Even though studies of caterpillar populations and assemblages frequently make use of both branch-beating (e.g.: Yela & Lawton, 1997; Mody & Linsenmair, 2004; Markó *et al.*, 2006) and visual searching/hand collecting (e.g. Novotny *et al.*, 2006; Dyer *et al.*, 2007) methods, studies that try to quantitatively assess their overall efficiency and possible biases are strikingly rare. Sampling of two species of *Piper* shrubs in the montane forest zone of southern Ecuador turned out to retrieve only slightly more than 50% of the caterpillars that were present on shrubs of *Piper* sp. I. Considering that especially some very small caterpillars will likely have been overlooked even during our high intensity leaf-by-leaf search, the real efficiency can probably be expected to be a bit lower and may be below 50% even for the combined sampling protocol. In the light of these results our hypothesis (1) that sampling retrieves the majority of caterpillars on a shrub can at best be cautiously accepted. Efficiency of sampling on simpler structured *Piper* sp. III was significantly higher, as predicted by hypothesis (2). More detailed analysis revealed that the increase in overall efficiency on this shrub species was almost entirely due to visual search. The fraction of caterpillars recovered by beating was also slightly higher, even though the fraction of caterpillars still remaining on the shrub at this stage is smaller, revealing that beating efficiency has also increased notably. While higher search efficiency is probably due to lower availability of hiding places and less visual distraction of the researcher, higher beating efficiency is likely due to the smoother leaf surface of *Piper* sp. III offering a less strong foothold to caterpillars.

Comparison of $cat_{(ss)}$ and $cat_{(es)}$ on higher taxonomical levels revealed a significant bias in two of the experiments, especially in P1 where only sampling by beating was performed. In both cases the bias was almost entirely due to caterpillars from the genus *Eois* being underrepresented in $cat_{(ss)}$. *Eois* species are small-sized and usually very specialized herbivores. The limited data presently available indicates that many species may even be limited to a single host plant species (e.g. Dyer *et al.*, 2010; Strutzenberger *et al.*, 2010). This could explain their reluctance to drop off the plant, since they are unlikely to find a suitable host plant again. Such a behavior would render them underrepresented in samples acquired by beating. Identification of the individual caterpillar specimens did not indicate any entirely new *Eois* species that would have been acquired only by subsequent defoliation (even though species accumulation of *Eois* in the study area is far from being complete: Strutzenberger *et al.*, in press). Consequently, although hypothesis (3) has to be discarded, the sampling bias is of a predictable nature and in a small range that appears to be acceptable, since no herbivore species were overlooked.

Caterpillar assemblages on larger shrubs were sampled less completely as compared to small shrubs, falsifying hypothesis (4). We had not increased sampling effort in linear fashion with shrub size since we had expected higher per-effort-efficiency for larger shrubs, i.e. more shrub biomass can be sampled by a single beat or searched visually by turning one branch. Evidently this expected effect has either been overestimated or canceled out at least partly by other effects. One possible negative size dependent influence is e.g. loss of recorder focus when visually searching larger numbers of leaves simultaneously. Beating efficiency on the other hand could be negatively influenced e.g. by tighter packing of branches and leaves, resulting in caterpillars shaken off from one leaf to land on another instead of the beating tray.

Samples taken under otherwise identical conditions during day and night did not significantly differ in any aspect, confirming hypothesis (5). This indicates that there is no reason to assume substantial day-to-night migrations of caterpillars on the sampled shrubs. Therefore caterpillar assemblages sampled during daytime should not be biased, e.g. due to missing nocturnal species. This confirms that the standardized sampling protocol is suitable for assessments irrespective of the time of day. However, we do not expect this to be necessarily true for other plant species, where diurnal migration of caterpillars might play a more important role (see e.g. Huogue, 1993).

Samples gathered by inexperienced field assistants did not significantly differ on a taxonomical basis from those taken by an experienced researcher and are therefore comparable and can be combined for analysis. Sampling efficiency was even calculated to be slightly higher for inexperienced assistants. This appears surprising at first glance, since one would suspect that experience in searching for caterpillars increases the number of caterpillars found during the same time during visual search at least. Closer examination of the size distribution of caterpillars collected during the experiments P2 and P3/I reveals, however, that the average size of all caterpillars ($cat_{(ss)}$ and $cat_{(es)}$ combined) was significantly larger on shrubs sampled by recorders without previous experience. This indicates that a larger fraction of small caterpillars was overlooked by inexperienced field assistants even during intensive leaf-by-leaf search. This also offers an explanation why the average number of caterpillars per shrub in both $cat_{(ss)}$ and even more so in $cat_{(es)}$ is lowest in experiment P3/I of the three experiments dealing with the plant species *Piper* sp. I. This leads to the conclusion that the efficiency of P3/I is particularly overestimated by the raw numbers and that the real efficiency is probably considerably lower for inexperienced field assistants as compared to experienced researchers.

Conclusions

We conclude that the two-staged sampling protocol presented in this study retrieved about half of the caterpillars which were in fact present on the sampled

Piper shrubs. While a taxonomic bias existed against well attached host-plant specialists, this bias was smaller than with beating alone and of a predictable nature. Overall sampling efficiency was only slightly increased by adding visual search to beating, possibly because the slight shaking of the shrub, which is unavoidable during search, caused caterpillars to hold on more tightly. However, besides the reduction in taxonomic bias, visual search also allows for the gathering of at least some part of the eggs, cocoons and pupae that would be completely overlooked by beating alone. Moreover, observations during visual research have the potential to yield information on behavior and functional connections between caterpillars and plants that are lost after beating. This includes the ability to distinguish between gregarious and solitary caterpillars. Sampling intensity has to be chosen in consideration of necessary sampling efficiency, but also with consideration of the size range of shrubs to be studied, lest sampling effort becomes unreasonably small or large at either end of the range. Linear increase of sampling effort might however lead to more homogenous sampling efficiency across shrub sizes.

Overall we consider the presented two-stage sampling protocol to be fairly suitable for studying caterpillar communities on shrubs, especially when resampling of the same shrub individuals in a time series is desired. At the same time the method is minimally invasive, since only the caterpillars present on the shrub at that time are affected and non-target animals can be freed again immediately.

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